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Sting Autotomy, Sting Morphology and Sociality in Neotropical Vespids (Hymenoptera: Vespidae)

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Abstract.—Autotomy of the sting apparatus was investigated in twenty eight species of neotropical social wasps belonging to the Polistinae. Sting autotomy was found to be positively correlated with the number of acuminate barbs and with the degree of sociality.

INTRODUCTION

The high degree of kinship among the cohabitants of social Hymenoptera colonies, their subsequent altruistic behavior and differential reproductive investment suggest that defense may have become progressively more important with in increasing sociability (Hermann & Blum 1981). According to Starr (1985, 1988), sting development occurred due to the pressure exerted by predators that were attracted by the increase in colony size, especially in tropical regions.

Some species of social Hymenoptera display autotomy of the sting apparatus. Although this process has been known since 1933, according to Rau (apud Hermann 1971), no comparative studies are available to support a discussion about its contribution to the evolution of socia-

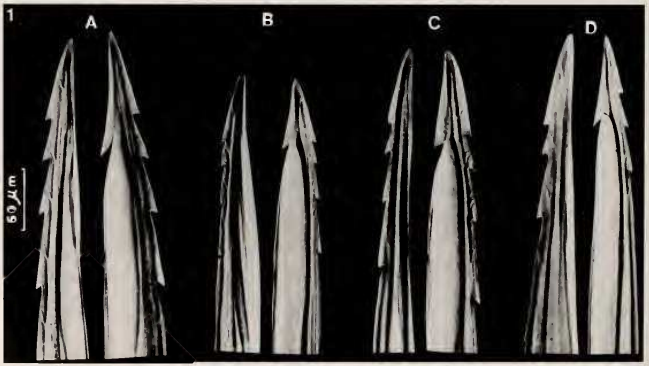

Fig. 1. Lancets of the stinging apparatus of the social wasps from genus *Mischocyttarus*. A. *M. drewseni*. B. *M. cassununga*. C. *M. latior*. D. *M. cerberus*.

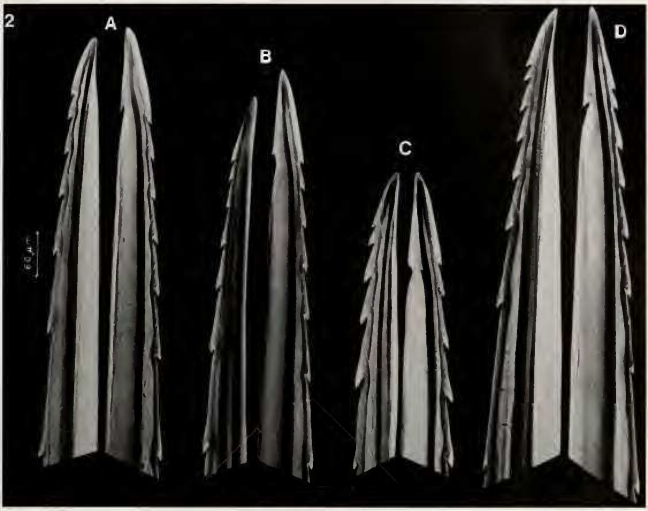

Fig. 2. Lancets of the stinging apparatus of the social wasps from genus *Polistes*. A. *P. versicolor*. B. *P. similimus*. C. *P. subsericeus*. D. *P. lanio lanio*.

bility among wasps. Hermann (1971), Poore (1974a, 1974b) and Hermann & Blum (1981) demonstrated the existence of barbs in the lancets of the stings of both solitary and social Hymenoptera and speculated that the shape and size of these barbs, in addition to other variables, must contribute in some way to the autotomy process.

In the present study we have investigated the sting autotomy in various species of social wasps of the subfamily Polistinae and report here correlation both with the degree of sociality as defined by Evans (1958), and with the morphology of sting in agreement with the predictions of Hermann (1971).

MATERIALS AND METHODS

The social wasps species studied were from the towns of Rio Claro, Ribeirão Preto and Pirassununga (State of São Paulo, southeastern Brazil) and from Belém (State of Pará, northern Brazil), as follow:

Agelaia pallipes pallipes (Olivier, 1791)
Agelaia vicina (de Saussure, 1854)
Agelaia multipicta (Halliday, 1836)
Polybia (Myrapetra) paulista H.von Ihering, 1896
Polybia (Apopolybia) jurinei de Saussure, 1854
Polybia (Myrapetra) occidentalis (Olivier, 1791)
Polybia (Trichothorax) sericea (Olivier, 1791)

Fig. 3. Lancets of the stinging apparatus of the social wasps from genus *Apoica*. A. *A. pallens*. B. *A. flavissima*.

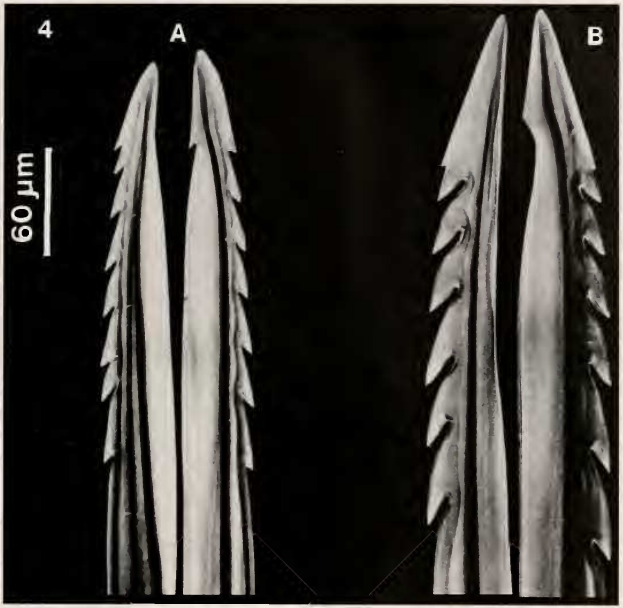

Fig. 4. Lancets of the stinging apparatus of the social wasps from genera *Metapolybia* and *Pseudopolybia*. A. *M. cingulata*. B. *P. vespiceps*.

Polybia (Myrapetra) platicephala slyvestris Richards, 1951
Polybia (Formicicola) rejecta (Fabricius, 1798)
Polybia (Myrapetra) scutellaris (White, 1841)
Polybia (Myrapetra) fastidiosuscula de Saussure, 1854
Protonectarina sylveirae (de Saussure), 1854
Brachygastra lecheguana (Latreille, 1824)
Metapolybia cingulata (Fabricius, 1804)
Pseudopolybia vespiceps (de Saussure, 1864)
Protopolybia sedula (de Saussure,1854)
Protopolybia exigua exigua (de Saussure, 1854)
Synoeca cyanea (Fabricius, 1775)
Apoica (Apoica) pallens (Fabricius, 1804)
Apoica (Apoica) flavissima Van der Vecht, 1973
Mischocyttarus (Haplometrobius) cerberus Ducke,1918
Mischocyttarus (Mischocyttarus) drewseni de Saussure, 1857
Mischocyttarus (Monocyttarus) cassununga (R. von. Ihering, 1903)

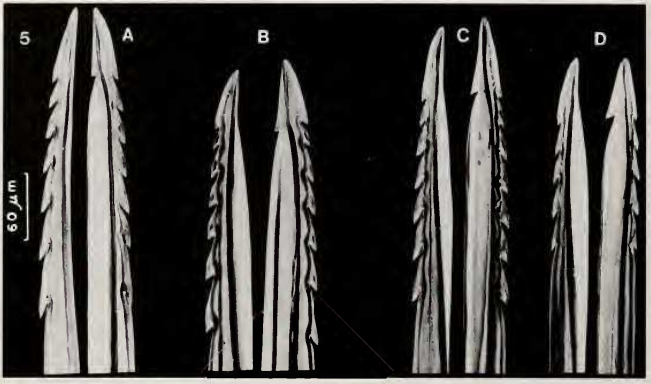

Fig. 5. Lancets of the stinging apparatus of the social wasps from genera *Brachygastra, Protonectarina* and *Protopolybia*. A. *B. lecheguana*. B. *P. sylveirae*. C. *P. sedula*. D. *P. exigua exigua*.

Mischocyttarus (Kappa) latior (Fox, 1898)
Polistes (Epicnemius) subsericeus de Saussure, 1854
Polistes (Aphanilopterus) versicolor (Olivier, 1791)
Polistes (Aphanilopterus) simillimus Zikan, 1951
Polistes (Aphanilopterus) lanio lanio (Fabricius, 1775).

Sting autotomy was investigated in twenty-eight species of Polistinae using the methodology of Stort (1974) and Overal *et al* (1981). Targets consisting of black suede balls 5 cm in diameter attached with a string to a 2.00 m long pole were dangled and shaken 15 cm from the entrance to the nest and allowed to be attacked. Thus, the species endowed with the autotomy process lose their stings which remain fixed to the target. The sting apparati of these species were dissected and the right and left lancets separated, dehydrated in 90 and 100% ethyl alcohol (I, II and III) and cleared in xylene (I, II and III). The lancets were cut in the middle for mounting and for better barb visualization, since the barbs are positioned laterally in the lancets. The lancet pieces containing the barbs were mounted on slides with Canada Balsam (Cruz-Landim & Beig 1966).

RESULTS AND DISCUSSION

In those social wasps that exhibit "sting autotomy", the venom reservoir and associated gland, various muscles and associated cuticular plates, as well as the sting proper are left attached to the victim's sting. As a consequence of this considerable damage, the individual wasp invariably dies soon, and afterwards so that the behavior might be thought in terms of "defensive altruism".

In all the wasps studied the left and right lancets we found to have several barbs (Figs. 1 to 9). There was some intraspecific variation and also some variation between left and right lancets. Anatomically, the left and right lancets differ both

Fig. 6. Lancets of the stinging apparatus of the social wasps *Synoeca cyanea*.

in thickness and in shape; the right lancet is wider from the median portion to the apex, which is shaped like an arrow positioned perpendicularly in relation to the barbs. The barbs are located on the external sides of the lancets and are distributed on the upper portion of the latter and may be either longer and of the acuminate type or shorter and of the serrated type.

The tables 1 and 2 are showing the recorded variation in the number of barbs/lancet for autotomisers and no autotomisers social wasps, respectively.

Even considering that are some species both with a reduced number of barbs among the autotomisers (Table 1) and species with large number of barbs among the non-autotomisers (Table 2), the direct comparison betweem these groups based on t-tests of means revealed that, overall, the number of bars/lancet were significatively higher ($P< 0,01$) in autotomisers. These results suggest that the morphology of sting is important character to the occurrence of the process of autotomy.

During the aggressivity tests no queen was identified among the aggressors. Some queens collected both in a specie which they are not morphologically distinct from workers, like *Polybia paulista*, and in species whose they are morphologically distinct from workers, like *Agelaia pallipes* and *Protonectarina sylveirae*; the morphology of theirs stings and the numbers of barbs were identical to those described for the workers. In spite to this similarity the queens do not attend the defense of their colonies. Overal *et al* (1981) also related the absence of queens during actions of colony defense in *Polybia rejecta*.

Among the autotomisers species the number of aggressors and stings left over the targets in each trial of the aggressivity tests, was very different from specie to specie. This aspect of the defensive answer must consider the level of sociability of each specie, which in turn seems to be influencing differentially the aggressive behavior of these species. As exemple of this influence, Manzoli—Palma (1993), observed that in spite of *Metapolybia cingulata and Polybia occidentalis*, present sting autotomy, during the tests of aggressivity the most individual of these colonies scaped away to a far place or hidden themself

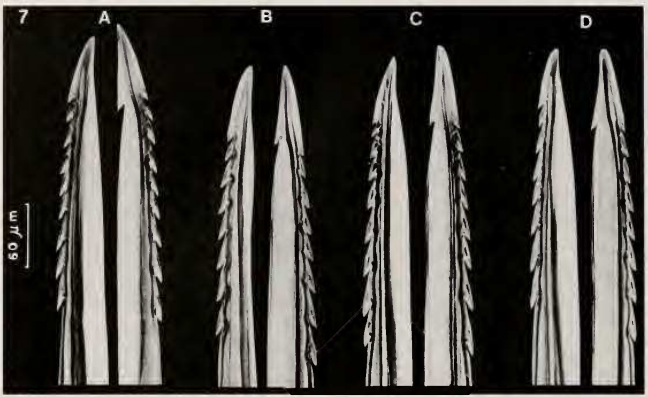

Fig. 7. Lancets of the stinging apparatus of the social wasps from genus *Polybia*. A. *P. paulista*. B. *P. platicephala sylvestris*. C. *P. scutellaris*. D. *P. occidentalis*.

inside the nest, rarely stinging the target or the experimenter. Thus, in this situation the number of aggressors and stings left over the targets were very small even after intense provocation.

According to West-Eberhard (1973) and Jeanne (1991) these species belong to the group that alternate between monogyny and polygyny. These species seems to opt preferentially for flight since they present small populations in which the loss of a single individual may be important. Thus, it would be of high adaptive value to maintain the malleability of the colony; in other words, in an emergency situation the population may abandon the nest as a whole, so that the occurrence of temporary polygyny will permit a rapid establishement of a new brood.

In addition to this, there are other aspects that may influence the level of aggressivity even from nest to nest of the same specie. The population structure of each colony at the moment of the tests, such as: the total number of adults (number of workers, queens and males), larvae and pupae are important factors that also must be considered. Thus, as exemple of the influence of these factors, Manzoli-Palma & Gobbi (1994) demonstrated in *Polybia paulista* that the number of aggressors and stings left over the targets, increases as function the increasing in the number of workers and is amazingly potentiated by an increasing in the number of pupae.

In general, the species that do not present autotomy of the sting apparatus belong to the tribes **Polistini** and **Polybiini**, whereas those that present such a process belong to a group from the tribe **Polybiini** which presents a higher degree of sociability (Evans 1958). Thus, it was observed that, the increase in the number and development of barbs only occurred after the establishment of greater social complexity, although independent of morphological female differentiation. Thus, the study of sting apparatus mor-

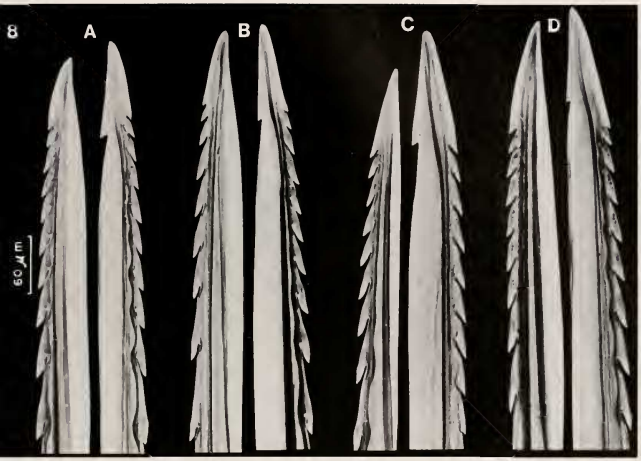

Fig. 8. Lancets of the stinging of the social wasps from genus *Polybia*. A. *P. fastidiosuscula*. B. *P. rejecta*. C. *P. sericea*. D. *P. jurinei*.

phology contributes to a better understanding of the probable extent of specialization of each genus.

When analyzing the relation between the level of sociability, autotomy process, nest architecture and number of barbs, the genus *Mischocyttarus* presents the smaller number of barbs that are less acuminate (Fig. 1) (barbs = 4), whereas the barbs of *Agelaia* are more pronounced and present in larger numbers (Fig. 9) (barbs = 9 to 14). These genera are located on the 11th and 13th steps of the evolutionary scale of Evans (1958), respectively, with well differentiated aggressive behaviors. Individuals of the *Mischocyttarus*, species observed by us adopted a posture of indifference in situations of danger, never stung the experimenter and at times abandoned the nest. This species present, social regulation via individual dominance, are monogynous, build opened nests, with small populations where a situation in which the loss of some individuals might be highly harmful to colony maintenance and/or continuity.

However, wasps of the genus *Agelaia* attack in groups, are extremely aggressive pursue the experimenter and easily lose their stings in the target. This species build nest inside a preexisting structure to shelter it, are polygynous, present large populations, swarm-founding and sometimes worker caste morphologically distinct from queen. For these neotropical wasp species, sting autotomy is a process that favors colony defense when the loss of some individuals is not significant for the colony as a whole. Thus, in danger situations such as attack by a predator, the sacrifice of some altruistic individuals for colony defense is preferable to the flight

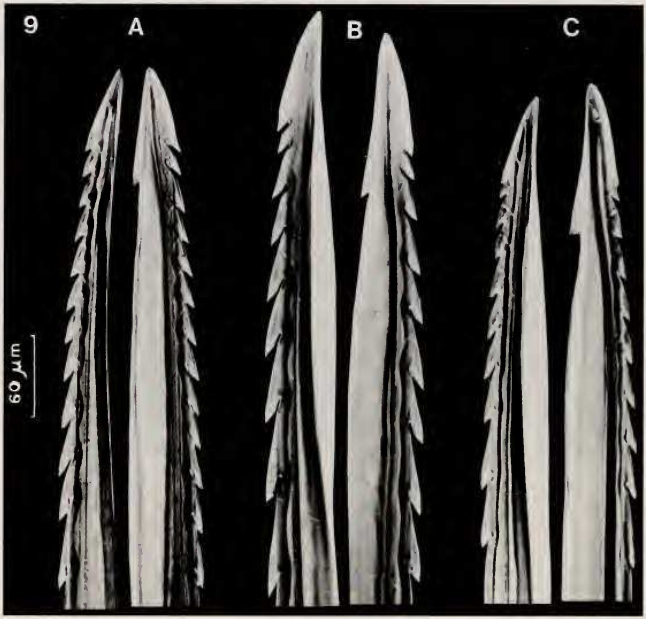

Fig. 9. Lancets of the stinging of the social wasps from genus *Agelaia*. A. *A. vicina*. B. *A. pallipes pallipes*. C. *A. multipicta*.

of the entire population in order to found a new nest.

Species that alternate between monogyny and polygyny still may produce more complex interactions between those factors that are influencing the occurrence of sting autotomy creating some exceptions in relation to the established patterns of autotomy. Thus, for exemple individuals of the genus *Apoica* that alternate between monogyny and polygyny (Gobbi, 1987; Shima, 1991), have some characteristics of autotomisers such as: large number of well developed barbs, large population and nests founding by swarm but have also a characteristics of non-autotomisers such as: nest with a single comb without envelop (Richards & Richards, 1951), but *Apoica pallens* did not show the autotomy process. After stinging a target, this species remains attached to it and fights intensely to try to escape, twisting its abdomen in circles and applying pressure to it with its legs. This causes some barbs to

Table 1. Variation in the number of barbs/lancet observed in social wasps that present sting autotomy.

Autotomisers			
Species	N	No. barbs/ lancet (Mean ± SD)	Range
Agelaia pallipes	80	9.8 ± 0.6	9–11
Agelaia multipicta	166	9.4 ± 1.1	8–10
Agelaia vicina	78	12.3 ± 0.9	11–14
Synoeca cyanea	32	11.5 ± 0.6	10–13
Polybia rejecta	52	9.2 ± 0.3	9–10
Polybia scutellaris	42	9.0 ± 0.4	8–10
Polybia fastidiosuscula	30	9.5 ± 0.6	8–11
Polybia jurinei	72	9.0 ± 0.1	8–10
Polybia paulista	264	8.9 ± 0.3	8–10
Polybia sericea	72	8.0 ± 0.1	7–9
Polybia occidentalis	62	8.0 ± 0.1	7–9
Polybia platicephala sylvestris	10	8.2 ± 0.3	8–9
Protonectarina sylveirae	50	6.8 ± 0.3	6–7
Brachygastra lecheguana	58	6.9 ± 0.3	6–7
Protopolybia sedula	124	7.0 ± 0.0	7
Protopolybia exigua	72	5.0 ± 0.2	4–6
Metapolybia cingulata	18	7.0 ± 0.1	6–8
Pseudopolybia vespiceps	52	6.9 ± 0.3	6–7

N = Number of lancets observed for each species.

break, permitting sting withdrawal and the aggressor escaping this is a different type of behavioral strategy. That adapts the insect to escape after stinging and would reduce the loss of individuals.

Thus, the results of the present work clearly show that sting autotomy in social wasps is correlated with morphological aspects which in combination with social and behavioral aspects form an altruistic defense system.

Table 2. Variation in the number of barbs/lancet observed in social wasps that not present sting autotomy.

Non-autotomisers			
Species	N	No. Barbs/ lancet Mean ± SD	Range
Apoica pallens	76	9.1 ± 0.2	9–10
Apoica flavissima	36	9.2 ± 0.4	9–10
Polistes versicolor	28	7.5 ± 0.9	7–8
Polistes lanio lanio	18	8.0 ± 0.0	8
Polistes subsericeus	18	5.1 ± 0.5	4–6
Polistes simillimus	20	7.1 ± 0.4	6–8
Mischocyttarus drewseni	16	4.0 ± 0.0	4
Mischocyttarus cassununga	20	4.0 ± 0.0	4
Mischocyttarus cerberus	18	4.0 ± 0.0	4
Mischocyttarus latior	22	4.0 ± 0.0	4

N = Number of lancets observed for each species.

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LITERATURE CITED

Cruz-Landim, C. and D. Beig. 1966. *Manual de laboratório para citologia, histologia e embriologia.* Rio Claro:UNESP-IB,SP, Brazil. 73p.

Evans, H. E. 1958. The evolution of social life in wasps. *Proceedings of 10th International Congress of Entomology.* 449–457.

Gobbi, N. 1987. Organização social em vespas (Hymenoptera: Aculeata). *Anais de Etologia* 5: 249–264.

Hermann, H. R. 1971. Sting autotomy, a defensive mechanism in certain social Hymenoptera. *Insectes Sociaux Paris,* 18 (2) 111–120.

Hermann, H. R and M. S. Blum. 1981. Defensive mechanism in the social Hymenoptera. In: H. R. Hermann, ed, *Social Insects.* New York: Academic Press, 2:491p.

Manzoli-Palma, M. F. 1993. Defesa da colônia, autotomia, morfologia comparativa do ferrão e suas implicações em Hymenoptera:Vespidae. Doctoral Thesis in Biological Sciences, Rio Claro: UNESP-IB, 133p.

Manzoli-Palma, M. F. 1994. Defesa da colônia na vespa social *Polybia paulista* (Ihering) (Hymenoptera: Vespidae). *Annais da Sociedade Entomológica do Brasil* 23 (2): 291–298.

Overal, W. L., D. Simões and N. Gobbi. 1981. Colony defense and sting autotomy in *Polybia rejecta* (F) (Hymenoptera: Vespidae). *Revista Brasileira de Entomologia* 25 (1): 41–47.

Poore, D. M. 1974a. Comparative Study of the lancets aand sheats of some Aculeata Hymenoptera. *Bulletin of the Southern California Academy of Sciences* 73 (1): 42–47.

Poore, D. M. 1974b. Sting Autotomy. *American Bee Journal* 114 (2): 57–61.

Richards, O. W. and M. J. Richards. 1951. Observations on the social wasps of South America (Hymenoptera,Vespoidea). *Transactions of the Royal Entomological Society of London* 102 (1): 1–169.

Shima, S. N. 1991. Variabilidade das castas em algumas espécies de vespas sociais (Hymenoptera,Vespidae, Polybiini). Doctoral Thesis in Biological Sciences, Rio Claro: UNESP-IB, 254p.

Starr, C. K. 1985. Enabling mechanisms in the origin of sociality in the Hymenoptera-The Sting` the thing. *Annals of the Entomological Society of America* 78 (6): 836–839.

Starr, C. K. 1989. In Reply, is the Sting the Thing? *Annals of the Entomological Society of America* 82: 6–8.

Stort, A.C. 1974. Genetic study of aggressiveness of two subspecies of *Apis mellifera* in Brazil. I Some tests to measure aggressiveness. *Journal of Apicultural Research* 13 (1): 33–38.

West-Eberhard, M. J. 1973. Monogyny in polygynous social wasps. *Proceedings of the 7th Congress of the International Union the Study of Social Insects*. 396–403.